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Erysiphe iranica sp. nov. on *Onobrychis caput-galli* in Iran

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Abstract—In April 2014, powdery mildew symptoms were found on *Onobrychis caput-galli* in Khan Ahmad, Gachsaran, Iran. Morphological characters and analysis of ITS and 28S rDNA sequences revealed that this powdery mildew does not match previously recorded species on fabaceous hosts. It is proposed as a new species, *Erysiphe iranica,* and is described and illustrated, and compared with previous species of powdery mildew recorded on *Fabaceae.*

Key words—biodiversity, *Erysiphaceae*, *Helotiales*, sainfoin, taxonomic novelty

Introduction

Species of *Onobrychis* Mill., also known as sainfoins, are Eurasian perennial herbs of the legume family (*Fabaceae*). This genus includes more than 130 accepted species and is the second largest genus in the tribe *Hedysareae* (Amirahmadi & al. 2016). The main center of diversity of sainfoins extends from Central Asia to Iran with 77 species of *Onobrychis* distributed throughout Iran (Amirahmadi & al. 2016). Based on the literature, at least 27 of these 77 species are endemic to Iran (Muzaffariyān 1996). East Azarbaijan province has the highest level of cultivation and amount of sainfoin forage production in Iran. Moreover, several species grow as wild plant throughout

the country. The nutritional benefits of *Onobrychis* spp. are almost the same as alfalfa. This forage is easily digested and does not cause bloating in animals (Gholami & al. 2017).

Forty-two species of *Erysiphe* sect. *Erysiphe* and *E.* sect. *Microsphaera* have been reported from *Fabaceae*, of which several species represent taxonomically complicated groups (Braun & al. 2010, Braun & Cook 2012, Bradshaw & al. 2021). The existence of intermediate morphological features among morphologically allied species, such as *E. baptisiicola* U. Braun, *E. bremeri* U. Braun, *E. viciae-unijugae* (Homma) U. Braun, *E. pisi* DC., and *E. trifoliorum* (Wallr.) U. Braun, may sometimes cast doubt upon correct identifications of the taxa involved. Most of these taxa have overlapping host ranges as well. Recently rDNA-ITS sequencing has addressed some of these questions (Kiss & al. 2020, Takamatsu & al. 2002, Meeboon & Takamatsu 2017, Bradshaw & al. 2021). Bradshaw & al. (2021) conducted a phylogenetic analysis on *Erysiphe* species colonizing hosts of the fabaceous genus *Lupinus*, using sequences from ITS and 28S rDNA genomic regions. They included several powdery mildew species infecting fabaceous plants. Although they could find solutions for some *Erysiphe* species on *Fabaceae*, the *E. trifoliorum* complex remained unresolved. Hence, ITS sequencing is not always sufficient, so that combinations of sequence data, and morphological and host range characteristics are necessary for correct identification. Moreover, multi-gene sequencing is underway for better understanding of taxonomically difficult complexes of powdery mildew fungi (Ellingham & al. 2019, Qiu & al. 2020). Hence, multi-locus sequencing is another tool that can be used to answer taxonomically complicated issues in this group of powdery mildews. There are only three species recorded on *Onobrychis* spp.: *Erysiphe astragali* DC., *E. pisi*, and *E. trifoliorum* (Braun & Cook 2012). The two latter species have been recorded on *O. caput-galli* from Iran (Azadbakht & al. 2013). In this study, *Erysiphe iranica* is introduced as a new species on *O. caput-galli* based on morphological as well as phylogenetic peculiarities.

Materials & methods

Morphological examination

Chasmothecia on infected leaves were analyzed using a needle, and asexual morphs using a clear adhesive tape. The asexual morphs were transferred into a drop of 1:1 lactic acid and glycerin on a microscopic slide, slightly heated, and then examined with a Sairan BM22 biological microscope. Asci, ascospores, and chasmothecial appendages were examined on a microscopic slide containing a drop of water. At least 20 chasmothecia, appendages, asci, ascospores, conidiophores, and conidia were

Table 1. Sequences of *Erysiphe* species and related taxa used in the analyses.

Species name	Voucher	Host	Location	ITS	LSU
Erysiphe astragali	HAL3356F (Epitype)	*Astragalus glycyphyllus*	Germany	MZ265151	MZ265151
	HAL3358F	*Astragalus glycyphyllus*	Germany	MZ265150	MZ265150
	MUMH:2585	*Astragalus glycyphyllus*	Ukraine	LC010052	LC010052
	MUMH:2590	*Astragalus glycyphyllus*	Ukraine	LC010055	LC010055
Erysiphe baeumleri	HAL3360F (Epitype)	*Vicia sylvatica*	Germany	MZ265152	—
	HAL3354F	*Vicia cracca*	Germany	MZ265153	MZ265153
	HAL3355F	*Vicia cassubica*	Germany	MZ265154	MZ265154
	HAL3357F	*Vicia sylvatica*	Germany	MZ265155	MZ265155
Erysiphe bremeri	IRAN 10810F	*Alhagi* sp.	Iran	AB104463	AB103077
Erysiphe diffusa	MUMH:3121	*Desmodium incanum*	Argentina	LC010060	—
	A.M.R. Almeida OILal	*Lupinus albus*	Brazil	EF196666	—
Erysiphe fallax	MUMH:4972	*Carica papaya*	Mexico	LC228608	LC228608
	FL-1	*Macroptilium lathyroides*	USA	MH560056	MH560056
Erysiphe glycines	MUMHJPN: 0396	*Desmodium laxum*	Japan	LC009948	LC009947
	HMNWAFU-CF2012031	*Vicia gigantean*	China	KR048063	KR048126
Erysiphe glycines var. *glycines*	MUMH1462	*Glycine max*	Japan	AB078807	AB078806
Erysiphe guarinonii	HAL 2337 F	*Baptisia australis*	Germany	MT524083	—
	MUMHJPN:1425	*Laburnum alpinum*	Switzerland	LC009983	—
	WTU-F-072448	*Baptisia australis*	USA	MT516325	—
Erysiphe intermedia	HAL3381F (Epitype)	*Lupinus polyphyllus*	USA	MZ265161	—
	HAL3385F	*Lupinus polyphyllus*	USA	MZ265162	—
	HAL3384F	*Lupinus rivularis*	USA	MZ265165	—
	HAL3389F	*Lupinus latifolius*	USA	MZ265167	—
	OE2015PMCS297	*Lupinus* sp.	UK	KY660904	—
Erysiphe iranica	**GUM 1805 (holotype)**	***Onobrychis caput-galli***	**Iran**	**OL709413**	**OL709411**

Species name	Voucher	Host	Location	ITS	LSU
Erysiphe lespedezae	HMUT 7043	*Bauhinia purpurea*	China	MF066655	MF066659
	HMUT 7042	*Bauhinia purpurea*	China	MF066654	MF066658
	HMUT 7041	*Bauhinia blakeana*	China	MF066653	MF066657
	HMUT 7040	*Bauhinia blakeana*	China	MF066652	MF066656
	HMNWAFU-CF2010359	*Lespedeza floribunda*	China	KR048068	KR048130
Erysiphe longissima	HMJAU91780	*Caragana rosea*	China	MH371103	MH371104
	HMJAU91781	*Caragana rosea*	China	MH371105	MH371106
Erysiphe ludens	OE2016PMCS45	*Lathyrus pratensis*	UK	KY661116	—
	OE2015PMCS298	*Lathyrus odoratus*	UK	KY660905	—
Erysiphe lupini	HAL3379F	*Lupinus polyphyllus*	USA	MZ265168	—
	HAL3380F	*Lupinus lepidis*	USA	MZ265169	—
	HAL3378F (Holotype)	*Lupinus* sp.	USA	MZ265170	—
Erysiphe medicaginis	BRIP 70957	*Medicago polymorpha*	Australia	NR_171870	—
	IRAN 10803F	*Medicago sativa*	Iran	AB104519	AB102942
Erysiphe palczewskii	MUMHJPN:1085	*Robinia* × *slavinii*	Japan	LC009974	LC009973
	MUMHJPN:s0111	*Robinia pseudoacacia*	?	LC010083	LC010083
Erysiphe pisi	OE2014PM137CS	*Pisum* sp.	UK	KY660822	—
	?	*Lathyrus latifolius*	?	AF011306	—
	MUMH:1850	*Pisum sativum*	Thailand	LC163915	—
	DNA03	*Pisum sativum*	Japan	LC009890	—
	OE2016PMCS80	*Pisum sativum*	UK	KY653209	—
	OE2016PMCS65	*Pisum sativum*	UK	KY653208	—
	OE2016PMCS81	*Pisum sativum*	UK	KY653210	—
	HUPS-11	*Pisum sativum*	China	MH143492	—
	Gh-01	*Pisum sativum*	?	MH290560	—
Erysiphe rayssiae	MUMHJPN:1433	*Baptisia australis*	Netherlands	LC009988	—

Species name	Voucher	Host	Location	ITS	LSU
Erysiphe robiniae	QHU2019007	?	?	MT309809	MT420267
Erysiphe robiniae var. *chinensis*	QHU2016095	?	?	MT309808	MT420266
Erysiphe sesbaniae	GUM777	*Sesbania punicea*	Iran	MF663776	—
Erysiphe sp.	Oidio-RB EI4	*Erythrina indica*	Brazil	MF326645	—
	Oidio-RB EI3	*Erythrina indica*	Brazil	MF326644	—
	Oidio-RB EI2	*Erythrina indica*	Brazil	MF326643	—
	NAUJA	*Trigonella foenum-graecum*	India	KY695255	—
	KRM0022477	*Lupinus micranthus*	Portugal	MZ265171	—
Erysiphe thermopsidis	QHU2018034	?	?	MT309725	MT309801
Erysiphe trifoliorum	MUMH:0701	*Trifolium arvense*	Hungary	LC009955	LC009954
	MUMH:7031	*Trifolium pratense*	Azerbaijan	LC270858	—
	?	?	?	FJ378877	—
	GH 05	*Pisum sativum*	USA	FJ378874	—
	KUS-F28516	*Trifolium hybridum*	South Korea	MN216307	MT380914
	KUS-F28551	*Trifolium hybridum*	South Korea	MN216308	—
	EI 08-2	*Pisum sativum*	USA	GU361634	—
	EI 08-1	*Pisum sativum*	USA	GU361633	—
	HAL3363F	*Lupinus polyphyllus*	Germany	MZ265172	MZ265172
	MUMH:7038	*Medicago littoralis*	Azerbaijan	LC270860	LC270860
Erysiphe viciae-unijugae	MUMHJPN:1159	*Vicia bifolia*	Japan	LC009977	LC009976
	MUMHJPN:0817	*Vicia angustifolia*	Japan	LC009962	LC009961
	MUMH:7040	*Lathyrus odoratus*	Azerbaijan	LC270861	LC270861
Pseudoidium sp.	MUMH 2587	*Coronilla varia*	Ukraine	LC010054	—
	MUMH 4935	*Crotalaria* sp.	India	AB522715	—
	MUMH 4934	*Brassica pekinensis*	India	AB522714	—
	MUMH 89	*Sophora flavescens*	Japan	LC009919	LC009919
Phyllactinia moricola	MUMH923	*Morus* sp.	Iran	AB080561	AB080459

examined. All photos were taken using a Leica DM 100 microscope equipped with a digital camera. The holotype specimen is conserved in the fungarium of the University of Guilan, Rasht, Iran (GUM).

Molecular phylogeny

The whole DNA was extracted using Chelex 100 method (Walsh & al. 1991). Powdery mildew specific primers PM10 (5′-GGCCGGAAAGTTGTCCAAAC-3′)/ PM11 (5′-TACCGCTTCACTCGCCGTTA-3′) were used to amplify the rDNA-ITS region (Bradshaw & Tobin 2020). Primer pairs RPM2 (5′-ACCTCAGTAACGGCGAGTGA-3′) (Bradshaw & Tobin 2020) and NLP2 (5′-GGTCCCAACAGCTATGCTCT-3′) (Mori & al. 2000) were used for the amplification of the 28S. The amplicons were sent to Codon Genetic Group, Tehran, Iran, to be directly sequenced by a 3500 Genetic Analyzer (Applied Biosystems, USA) using the forward primers mentioned above. The sequences were submitted to NCBI under the accessions OL709413 (ITS)/OL709411 (LSU).

Afterwards, similar sequences were obtained from NCBI (Table 1) and aligned using MUSCLE (Edgar 2004) implemented in MEGA7 (Kumar & al. 2016). Alignments were further manually refined using the MEGA7 program. Phylogenetic trees were obtained from the data using the Maximum Likelihood (ML) method. *Phyllactinia moricola* (AB080561) was set as the outgroup taxa. The ML analysis was done using raxmlGUI (Silvestro & Michalak 2012), under a GTRGAMMA model. The bootstrap analysis (Felsenstein 1985) consists of 1000 pseudoreplicates followed by a search for the tree with the highest likelihood.

Taxonomy

Erysiphe iranica Darsaraei, Khodap. & Pirnia, sp. nov. Figs 1–3

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Differs from *E. baptisiicola* by its shorter conidiophores with fewer cells following the foot-cell, fewer ascospores, and having hyaline appendages; and from *E. pisi* by its shorter conidiophores, conidia, and hyaline appendages.

Type: **Iran**, Kohkiluyeh & Boyerahmad province, Gachsaran, Khan Ahmad, on *Onobrychis caput-galli* (L.) Lam. (*Fabaceae*), 1 Apr. 2014, coll. Y. Behrooz (**Holotype**, GUM 1805)

Etymology: *iranica* refers to its origin in Iran.

Mycelium amphigenous, mostly hypophyllous, effuse. Hyphal cells 4–6 µm wide. Hyphal appressoria unlobed to lobed, solitary, rarely in opposite pairs. Conidiophores erect, arising centrally from the mother cell, 40–80 µm long. Foot-cells cylindrical, 32–40 × 6–13 µm, often sinuous at the basal part, followed by 1–2 shorter cells, forming conidia singly. Conidia ellipsoid, ovoid, cylindrical, occasionally adhering in false chains containing two conidia, 26–36 × 10–16 µm. Conidial germination terminal or sub-terminal. Germ tube

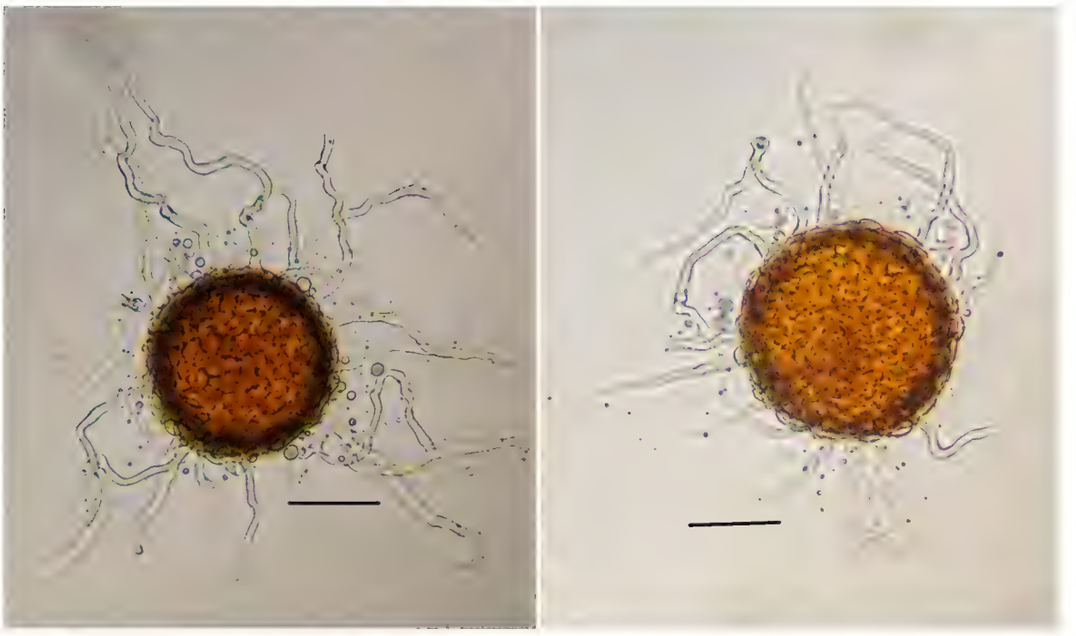


Fig. 1: *Erysiphe iranica* (holotype, GUM 1805). Chasmothecia. Scale bars = 50 µm.

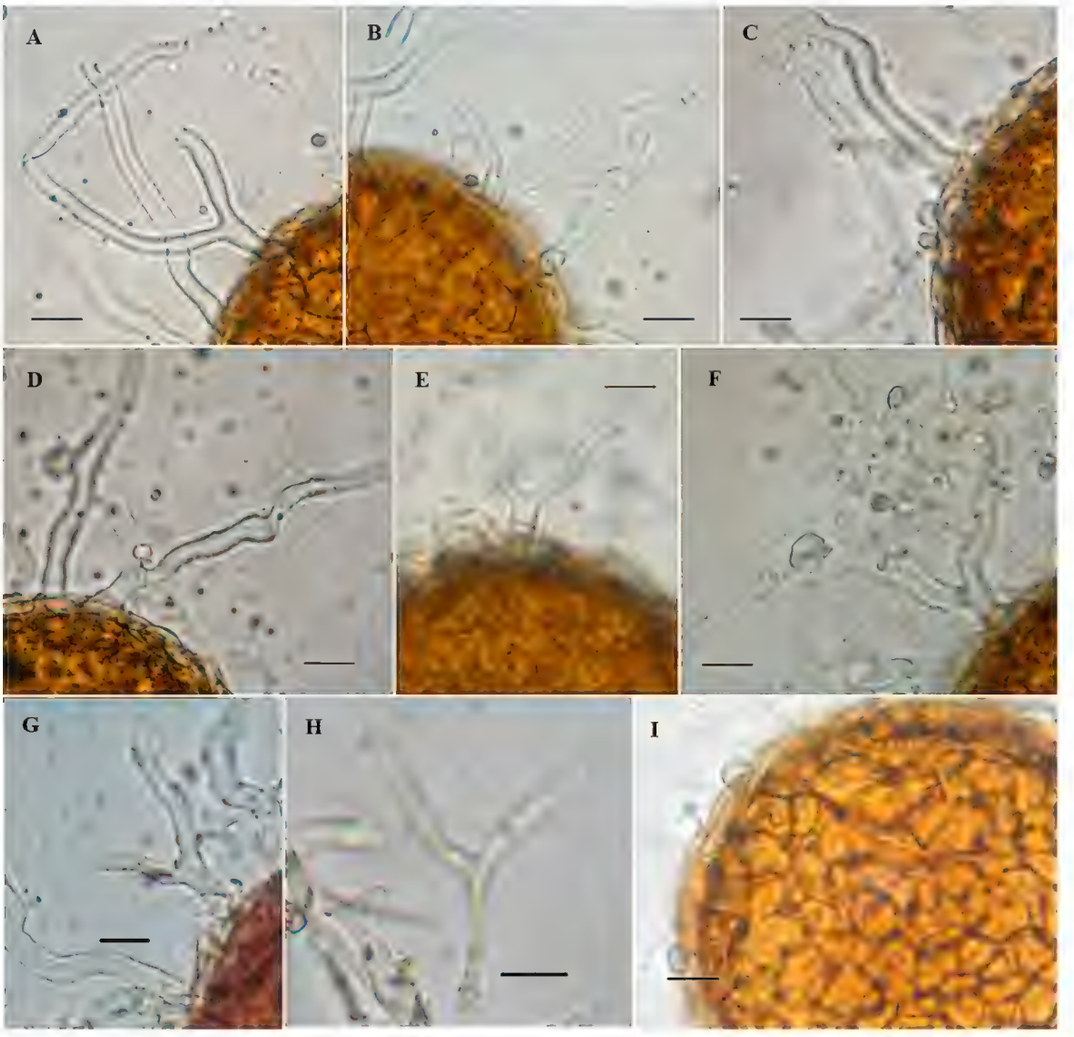


Fig. 2: *Erysiphe iranica* (holotype, GUM 1805).
A–H. Appendages; I. Peridium cells. Scale bars = 10 µm.

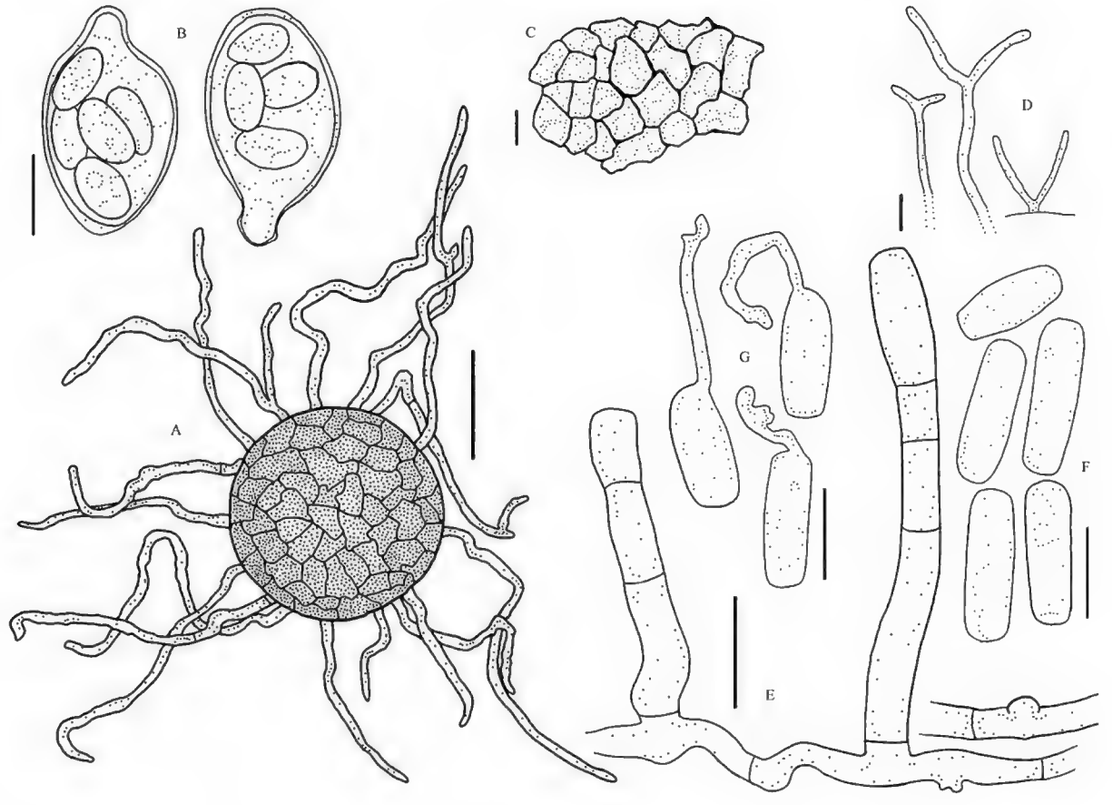
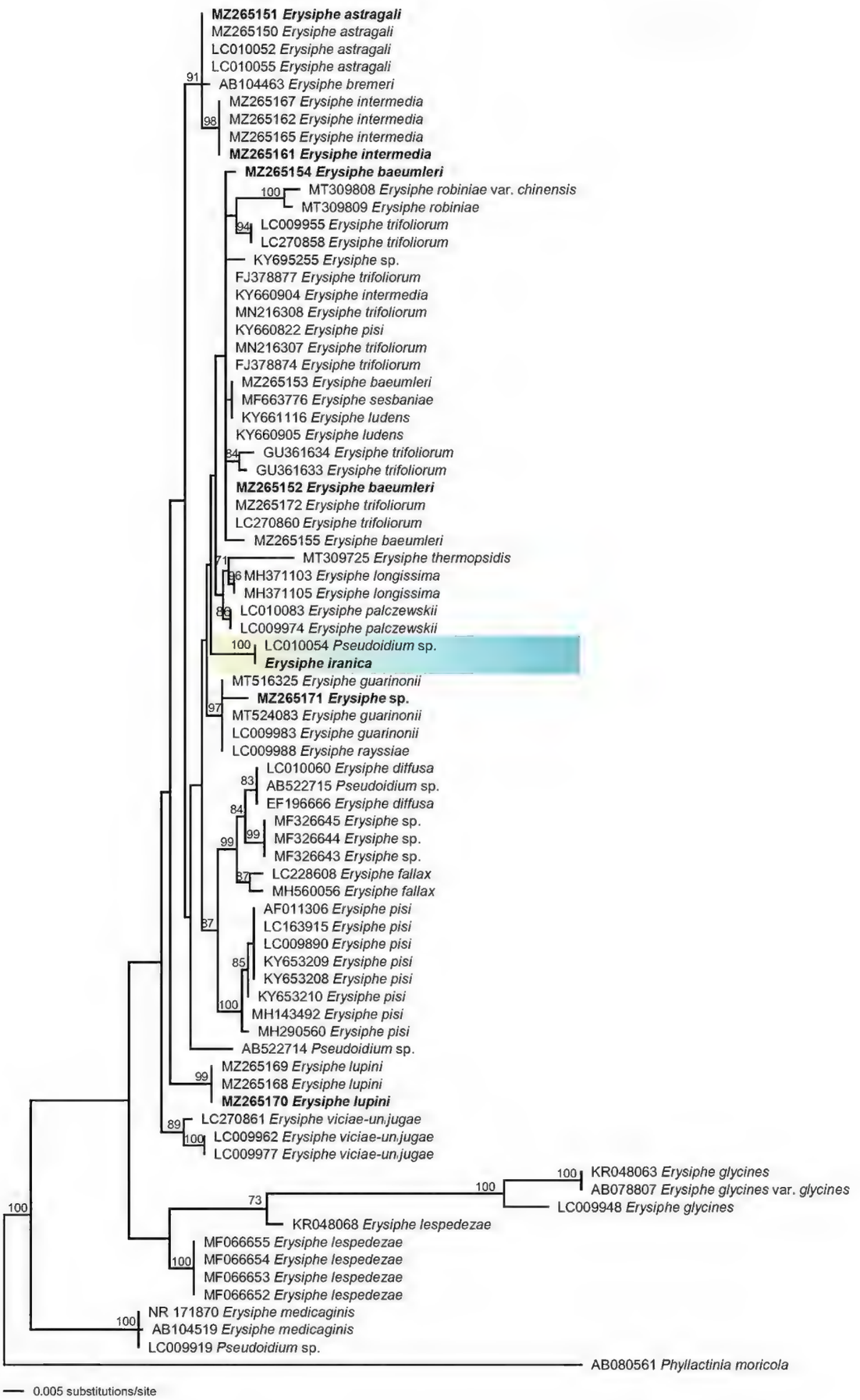


Fig. 3: *Erysiphe iranica* (holotype, GUM 1805). A. Chasmothecium; B. Asci; C. Peridium cells. D. Tips of appendages; E. Conidiophores and hyphal appressoria; F. Conidia; G. Conidial germ tubes. Scale bars: A = 50 µm; B, E-G = 20 µm; C, D = 10 µm.

up to 150 µm long. Chasmothecia amphigenous and caulicolous, scattered to ± gregarious, (85–)95–125 µm diam. Peridium cells conspicuous, irregularly polygonal, 8–25 µm diam. Appendages equatorial and somewhat in the lower half, hyaline, ~10–25, myceloid, occasionally slightly geniculate or angularly bent, sinuous, flexuous, occasionally forked, forming branches near the base or towards the tip, branchlets may be symmetric or not, occasionally with inconspicuous septa, about 0.5–2.5 times as long as the chasmothecial diam., width 12–20 µm at the very base, then 4–5 µm throughout, wall thin, almost equal throughout, smooth to ± rough. Asci 4–6, saccate-clavate, short-stalked to almost sessile, 48–67 × 27–38 µm, 3–5-spored. Ascospores ellipsoid, with oil drops, 15–23 × 8–13 µm, colorless or rather faintly yellow.

Fig. 4: Phylogenetic analysis of combined data of the 5′-end of the LSU rDNA and ITS region for 77 sequences from *Erysiphe* spp. on *Fabaceae*, including *Erysiphe iranica* and an outgroup sequence. BS values >70% by the maximum likelihood method are shown on the branches. Evolutionary analyses were conducted in raxmlGUI. Sequences from this study and from type materials are indicted by bold-face type.


MZ265151 Erysiphe astragali
MZ265150 Erysiphe astragali
LC010052 Erysiphe astragali
LC010055 Erysiphe astragali
AB104463 Erysiphe bremeri
MZ265167 Erysiphe intermedia
MZ265162 Erysiphe intermedia
MZ265165 Erysiphe intermedia
MZ265161 Erysiphe intermedia
MZ265154 Erysiphe baeumleri
MT309808 Erysiphe robiniae var. chinensis
MT309809 Erysiphe robiniae
LC009955 Erysiphe trifoliorum
LC270858 Erysiphe trifoliorum
KY695255 Erysiphe sp.
FJ378877 Erysiphe trifoliorum
KY660904 Erysiphe intermedia
MN216308 Erysiphe trifoliorum
KY660822 Erysiphe pisi
MN216307 Erysiphe trifoliorum
FJ378874 Erysiphe trifoliorum
MZ265153 Erysiphe baeumleri
MF663776 Erysiphe sesbaniae
KY661116 Erysiphe ludens
KY660905 Erysiphe ludens
GU361634 Erysiphe trifoliorum
GU361633 Erysiphe trifoliorum
MZ265152 Erysiphe baeumleri
MZ265172 Erysiphe trifoliorum
LC270860 Erysiphe trifoliorum
MZ265155 Erysiphe baeumleri
MT309725 Erysiphe thermopsidis
MH371103 Erysiphe longissima
MH371105 Erysiphe longissima
LC010083 Erysiphe palczewskii
LC009974 Erysiphe palczewskii
LC010054 Pseudoidium sp.
Erysiphe iranica
MT516325 Erysiphe guarinonii
MZ265171 Erysiphe sp.
MT524083 Erysiphe guarinonii
LC009983 Erysiphe guarinonii
LC009988 Erysiphe rayssiae
LC010060 Erysiphe difusa
AB522715 Pseudoidium sp.
EF196666 Erysiphe difusa
MF326645 Erysiphe sp.
MF326644 Erysiphe sp.
MF326643 Erysiphe sp.
LC228608 Erysiphe fallax
MH560056 Erysiphe fallax
AF011306 Erysiphe pisi
LC163915 Erysiphe pisi
LC009890 Erysiphe pisi
KY653209 Erysiphe pisi
KY653208 Erysiphe pisi
KY653210 Erysiphe pisi
MH143492 Erysiphe pisi
MH290560 Erysiphe pisi
AB522714 Pseudoidium sp.
MZ265169 Erysiphe lupini
MZ265168 Erysiphe lupini
MZ265170 Erysiphe lupini
LC270861 Erysiphe viciae-unijugae
LC009962 Erysiphe viciae-unijugae
LC009977 Erysiphe viciae-unijugae
KR048063 Erysiphe glycines
AB078807 Erysiphe glycines var. glycines
LC009948 Erysiphe glycines
KR048068 Erysiphe lespedezae
MF066655 Erysiphe lespedezae
MF066654 Erysiphe lespedezae
MF066653 Erysiphe lespedezae
MF066652 Erysiphe lespedezae
NR 171870 Erysiphe medicaginis
AB104519 Erysiphe medicaginis
LC009919 Pseudoidium sp.
AB080561 Phyllactinia moricola
0.005 substitutions/site

Discussion

Molecular phylogeny

A total of 78 sequences comprising 1224 characters were included in the phylogenetic analysis. *Erysiphe iranica* differed from a *Pseudoidium* sp. (MUMH 2587, LC010054) from Ukraine by only two bases (one substitution; one indel) in the ITS sequence, and by only one base (indel) in the 28S sequence. The next closest hit for the ITS sequence was *E. trifoliorum* (LC270860, identities 682/695, Abasova & al. 2018). We observed 19 substitutions in nucleotide sequences of *E. iranica* compared with another closely related species, *E. diffusa* (Cooke & Peck) U. Braun & S. Takam.

Erysiphe iranica and *Pseudoidium* sp. formed a distinct clade with 100% BS support (Fig. 4).

Morphology

Among the 42 *Erysiphe* species on *Fabaceae,* some (e.g., *E. trifoliorum* and *E. pisi*) are undoubtedly complexes of several taxa and are morphologically and genetically (according to the ITS sequence) almost indistinguishable. The rDNA ITS and 28S sequences from *E. iranica* are clearly separated from other available sequences retrieved from powdery mildew species on *Fabaceae*. The only sequence with greater than 99.6% identity with *E. iranica* on *Onobrychis* was *Pseudoidium* sp. (MUMH 2587) on *Securigera varia* [≡ *Coronilla varia*], but morphological data for this anamorphic specimen is unavailable. *Onobrychis* (*Fabaceae* tribe *Hedysareae*) and *Securigera* (*Fabaceae* tribe *Loteae*) are not closely allied, which suggests that *E. iranica* may have a wider host range within *Fabaceae.*

Erysiphe iranica is also morphologically distinct, with relatively few similar species. *Erysiphe baptisiicola* has longer conidiophores, more cells (1–3) above the foot-cell, more ascospores, and pigmented appendages that are thick and smooth to (usually) distinctly verruculose. *Erysiphe pisi* differs in its longer and pigmented appendages and longer conidiophores and conidia. We conclude that *E. iranica* on *Onobrychis caput-galli* from Iran is morphologically distinct from all previously described *Erysiphe* species on *Fabaceae*; and the combination of its morphological and molecular differences justifies its proposal as a new species.

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